

Research Article

Social and Environmental Drivers of Black-Necked Crane (BNC) Habitat Suitability in Bhutan: Insights From Maxent Modelling and Conservation Implications

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The conservation of Bhutan's Black-Necked Cranes (BNC) began in 1986 under the Forest and Nature Conservation Act of 1995, prioritizing habitat enhancement, community involvement, and scientific research. Employing the Maxent-LQH model, we comprehensively assessed BNC habitat suitability in Bhutan, selecting 10 environmental variables based on their AIC. Our analysis, utilizing a dataset of 23 occurrence records, identified key determinants such as distance to settlements, NDVI, roads, and rivers, impacting habitat suitability. The spatially confined suitable habitat area for BNC in Bhutan encompasses 549 km², accounting for 1.44% of the nation's land area, with secondary variables contributing modestly. While validation metrics (AUC = 0.98, TSS = 0.83) demonstrate high accuracy, acknowledging methodological limitations is essential. Furthermore, integrating these insights into conservation strategies is crucial, advocating for the extension of existing conservation zones and identifying novel areas for conservation. These findings underscore the critical role of environmental determinants in shaping BNC distribution patterns, necessitating tailored conservation efforts to protect this endangered species and its habitat in Bhutan.

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Abbreviations

Acronyms	Abbreviations
AUC	Area under the Curve
BNC	Black Necked Crane
DEM	Digital Elevation Model
DoFPS	Department of Forest and Park Service
FEMD	Flood Engineering and Management Division
HSI	Habitat Suitability Index
IUCN	International Union for Conservation of Nature
LULC	Landuse Landcover
MoIT	Ministry of Infrastructure and Transport
NDVI	Normalized Difference Vegetation Index
NLCS	National Land Commission Secretariat
RGoB	Royal Government of Bhutan
ROC	Receiver Operating Characteristic Curve
RSPN	Royal Society and Protection Nature
SDM	Species Distribution Model
SRTM	Shuttle Radar and Topography Mission
TSS	True Skill Statistics
USGS	US Geological and Survey

Keywords: black necked crane; species distribution model; Maxent; habitat suitability assessment; Bhutan.

1. Introduction

The black-necked crane (herein referred to as BNC), scientifically classified as *Grus nigricollis*, represents a distinguished avian species endemic to the high-altitude regions of Central Asia (BirdLife International, 2023). This species stands out as one of the rarest cranes globally, bearing significant cultural and ecological importance within

its native habitats. Renowned for its resplendent aesthetics, graceful movements, and intricate mating rituals, the BNC epitomizes a species of remarkable ornithological significance. Characterized by its distinctive habitat preferences, the BNC predominantly inhabits high-altitude wetlands, including marshes, meadows, and river valleys situated at elevations ranging from 2,400 to 4,800 metres above sea level (Dong et al., 2016). This unique habitat selection further underscores the species' ecological specialization within specific altitudinal zones, contributing to its rarity and vulnerability (Bai et al., 2022). Adapted to survive in harsh environmental conditions, such as exceedingly low temperatures and strong winds, the BNC exhibits features such as dense plumage and feathered toes for adept navigation through snow-laden and icy terrains. Notably, for extensive migratory behaviors, these avian species traverse substantial distances between their breeding and wintering grounds (Qian et al., 2009). Primarily herbivorous, BNCs sustain themselves through the consumption of diverse plant materials, including tubers, roots, seeds, and grasses, and during the breeding season, their dietary habits expand to include insects and small invertebrates, fulfilling additional nutritional requirements (Dong et al., 2016; Meine & Archibald, 1996). The dietary preferences of BNCs are intricately linked to the availability of food sources within their habitat, underscoring their pivotal role in the ecosystem (Wangchuk et al., 2023). In addition to their sustenance, they contribute significantly to seed dispersal and nutrient cycling, thereby exerting a crucial influence on the ecological dynamics of their environment (Meine & Archibald, 1996).

In addition to ecological considerations, the BNC holds substantial cultural significance within the geographic regions of its habitat and is revered by local communities as a symbol of good fortune, longevity, and fidelity (Letro et al., 2021). This cultural reverence is evident in the dedication of traditional festivals and rituals to their honour, emphasizing the imperative for conservation efforts. In a broader context, the BNC emerges as a captivating avian species embodying the intricate interplay between ecological resilience and cultural heritage (Phuntsho & Tshering, 2014). The conservation of these remarkable creatures and their habitats assumes a pivotal role in broader biodiversity preservation endeavors, contributing to the maintenance of the intricate tapestry of our natural world, safeguarding the dual objectives of ecological conservation and the preservation of cultural heritage (M. Li et al., 2022).

In terms of conservation status, BNCs have been classified as vulnerable by the IUCN according to BirdLife International, (2023). The primary threats jeopardizing survival include habitat degradation resulting from infrastructure development, agricultural expansion, and mining activities (Meine & Archibald, 1996; Parvaiz, 2018; and Yang et al., 2023). Furthermore, climate change-induced alterations in the availability of suitable habitats and food sources present formidable challenges to the long-term viability of these plants. Initiatives to safeguard the BNC and its delicate habitat are underway and are led by collaborative endeavors involving local communities, conservation organizations, and governmental entities. These conservation measures encompass the establishment of protected areas, the implementation of community-based conservation programs, and the dissemination of awareness regarding the importance of preserving these major avian species (DoFPS, 2021). International collaborations have been forged to facilitate knowledge sharing and the implementation of conservation strategies

spanning the entire range of the black-necked crane. These concerted efforts underscore the multifaceted approach essential for the preservation of the species and its habitat in the face of mounting anthropogenic and environmental threats.

The evaluation of habitat suitability for the BNC necessitates a comprehensive analysis aimed at assessing the appropriateness of habitats and environmental conditions conducive to species survival and reproductive success, as outlined by Phillips et al., (2006). This multifaceted assessment involves meticulous consideration of various factors that collectively define the ecological landscape supportive of the life cycle activities of BNC, including climate, nesting sites, human activity disturbance, conservation efforts, habitat requirements, food, and water availability. To discern suitable habitat features, an HIS model serves as a tool for evaluating habitat quality and identifying the spatial distribution of suitable habitat (Na et al., 2018; Van der Lee et al., 2006). Empirical SDMs have been developed to predict species distributions by correlating species occurrence with surrounding habitat features, providing a nuanced approach to assessing habitat suitability. Among the widely used species distribution models (SDMs), the maximum entropy (Maxent) stands out due to its unique approach and outstanding performance (Elith, 2008). Due to its nonparametric flexibility in handling complex species-environment relationships, resistance to overfitting, and overall high predictive performance validated across many habitat modelling applications, Maxent has rapidly become one of the most widely used niche modelling tools (Merow et al., 2013; Phillips & Dudík, 2008; Radosavljevic & Anderson, 2014). Therefore, to predict the distribution of and suitable habitats for species of conservation concern, we applied Maxent modelling based on its ability to make accurate and unbiased predictions from limited presence-only data. Occurrence records were combined with relevant climatic, topographic, and land cover predictor layers to model suitability and determine the environmental factors that had the greatest influence on the geographic distributions.

1.2. Historical background

The conservation of BNC in Bhutan started as early as 1986, and the highest protection was provided under Schedule I of the Forest and Nature Conservation Act, 1995. Recently, efforts have been made toward habitat improvement, enhancing community support and research (DoFPS, 2021). However, the population of BNCs is presumed to be decreasing, and considering the numerous threats from changes in agricultural practices, infrastructural development, and climate change, the BNC is listed as vulnerable in the IUCN Red List of Threatened Species (M. Li et al., 2022). In Bhutan, historical reports from elderly people suggest that large numbers of BNCs once wintered in Paro, Bajo in Wangduephodrang, and Chokhor Valley in Bumthang (Lhendup & Webb, 2010; Namgay & Wangchuk, 2016). Undoubtedly, the declining number of cranes visiting these areas can be partially attributed to human disturbance and development that altered suitable wintering habitats. In Bhutan, BNC conservation is limited by limited research and resources, increasing threats from infrastructure development, changing land use patterns and agricultural practices, predation by stray dogs, eutrophication of wetlands, and climate change (Letro et al., 2021; RSPN, 2020).

A small population of approximately 600 BNCs migrates to several valleys in Bhutan every winter between October and March (Phuntsho & Tshering, 2014). BNCs are protected throughout Bhutan, as they are listed under Schedule I as a protected bird species according to both the Forest and Nature Conservation Act of Bhutan, 1995 (RGoB, 1995) and the Forest and Nature Conservation Rules of Bhutan, 2017 (DoFPS, 2017). Recognizing the importance of the habitat for wintering cranes, the RGoB designated the Phobjikha Valley as a Conservation Area in 1999, with the RSPN serving as the focal agency for management, and the second most important habitat came under strict protection with the establishment of the Bumdeling Wildlife Sanctuary in 1995 (Letro et al., 2021). Phobjikha in the west, Bumthang in the central region, and Bumdeling in the east are the main wintering habitats for BNCs in Bhutan (Lhendup & Webb, 2010; Namgay & Wangchuk, 2016). Among these three populations, Phobjikha hosts the highest number of wintering cranes, with 473 individuals out of the total 555 national counts of the 2018–2019 winter. In the same winter month, Bumdeling Valley in the Tashiyangtse district was followed by 119 individuals (RSPN, 2019). A notable ecological phenomenon in Bhutan is the seasonal migration of approximately 600 BNCs, which occurs every winter between October and March (RSPN, 2020).

2. Materials and methods

2.1. Study area

Bhutan, which is situated in the eastern Himalayas, is a landlocked country that shares borders with China to the north and India to the south, west, and east, covering a geographic area of 38,394 km². Remarkably, approximately half of Bhutan's total land area (51.44%) is designated as a protected area network (PAN), comprising five national parks, four wildlife sanctuaries, one strict nature reserve, and eight biological corridors (BC) (Lham et al., 2021). Known for its predominantly mountainous terrain and deep river valleys, Bhutan exhibits a significant elevation gradient ranging from 92 m in the south to 7276 m above sea level in the north (Figure 1). This elevational diversity contributes to high floral and faunal diversities within the country (Tempa et al., 2021). The faunal diversity encompasses 129 mammalian species, including apex predators such as the tiger (*Panthera tigris*), common leopard (*Panthera pardus*), dhole (*Cuon alpinus*), snow leopard, and the endangered BNC (Thinley et al., 2017). The strategic location of these habitats underscores the ecological significance of Bhutan as a critical region for the conservation of the endangered BNC.

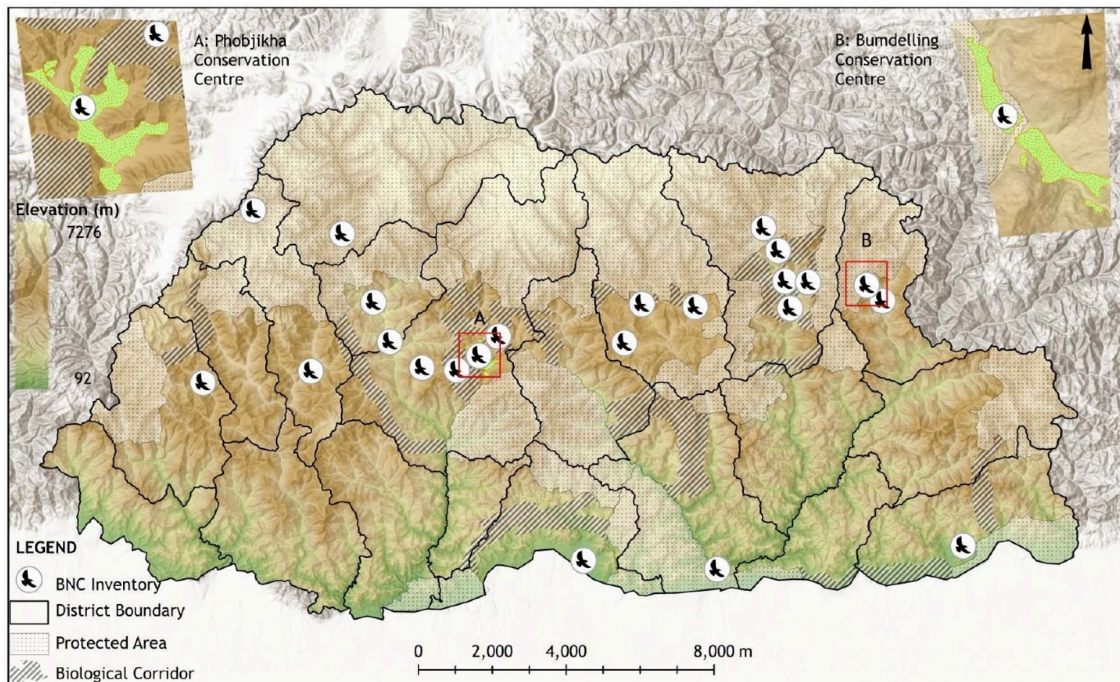


Figure 1. The biological corridors, protected areas, and elevation ranges. The inventory location and the conservation center of the BNC are demarcated by a red box. Two areas were identified as conservation centres for BNC according to (RSPN, 2020).

2.2. Data collection

2.2.1. Historical Inventory

Subsequent to the conclusion of the winter migration, the RSPN orchestrates a synchronized census, aiming to ascertain the comprehensive count of BNCs observed throughout the nation across diverse habitats (RSPN, 2019). This census serves as a pivotal tool for elucidating the population trends of crane species. Notably, the crane roosting sites were systematically surveyed during the census activities. The annual counts for distinct seasons were conducted in varying years and at different junctures; for instance, in 2014, the enumeration transpired on January 17, 2014, at 6:00 a.m. (RSPN, 2021). This specific time was selected extensively by stakeholders, including the Bomdeling Range Office, the Wangchuck Centennial Park, the Ugyen Wangchuck Institute for Conservation and Environment, the Forest Beat Office, and the Gangtey Aman Kora Resort in Phobjikha (Letro et al., 2021). Considering the fundamental importance of BNC location data in determining the correlation between BNCs and the causal factors impacting their habitat, species occurrence data were systematically collated from the RSPN amassed from 2003 to 2023.

2.2.2. Environmental Variables

Climate change poses a major threat to insect species survival, especially for habitat specialists, who are forcing vulnerable populations into an evolutionary race to adapt to changing conditions or, if accessible corridors exist, to shift their geographical ranges by tracking the movements of suitable habitats—neither of which are guaranteed rescue strategies under rapid anthropogenic warming (Lu et al., 2020). Deriving bioclimatic factors from monthly temperature and rainfall data yields crucial variables for simulating species distributions and ecological modelling. These indicators encompass seasonality, extreme environmental elements, annual trends, and temperature/precipitation ranges (see Table 1). Nineteen bioclimatic variables were extracted from the WorldClim data (30 arc-second resolution given in Table 2) and were tailored to Bhutan's geographic extent (26.45°N to 28.10°N; 88.45°E to 92.10°E). The dataset was projected onto the DRUKREF 03 Bhutan National Grid and resampled to a 1 km resolution using the raster package in R to ensure alignment with study-specific spatial and resolution requirements.

Acronyms	Climatic variable
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermally (BIO2/BIO7) *100
BIO4	Temperature Seasonality (Standard Deviation *100)
BIO5	Maximum Temperature of warmest Month
BIO6	Minimum Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5–BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter

Table 1. Bioclimatic variables obtained from WorldClim

2.2.3. Geomorphic and Foraging Conditions and Anthropogenic Types

The geomorphic attributes, encompassing elevation, slope, and aspect, were derived from SRTM data sourced from the United States Geological Survey (USGS) at a spatial resolution of 30 m. These data were subsequently resampled to a coarser spatial resolution of 1 km to facilitate analyses consistent with other raster data. Foraging conditions were characterized by the NDVI and proximity to water bodies, specifically rivers (Borowik et al., 2013). The NDVI data were derived from three Landsat 8 Operational Land Imager (OLI) tiles. River proximity was determined by

delineating stream flow from the DEM data, followed by Euclidean distance calculations using ArcGIS to ascertain the distance from the rivers.

Human activities were quantified through considerations such as proximity to roads, proximity to settlements, and land-use classifications (refer to relevant data sources in Table 2). Euclidean distance computations, standardized to a 1 km spatial resolution, were employed to gauge the distance from both roads and settlements, facilitating the integration of human influence metrics into the broader analytical framework.

Data	Sources
Occurrence inventory	www.rspnbhutan.org
Bioclimatic Variables	www.worldclim.org
Landsat 8 OLI	https://earthexplorer.usgs.gov/
Digital Elevation Model (DEM)	
Road Networks	MoIT (https://www.gov.bt/ministry-of-infrastructure-and-transport-3/)
Settlements	
Land use Land cover	NLCS

Table 2. Sources of variables used for modelling.

2.3. Data Processing and Parameter Optimization

2.3.1. Optimization of the Occurrence Point

To avoid overfitting and improve predictive performance, spatial filtering was applied to the occurrence point data in R Studio prior to model development. Specifically, we implemented a raster-based thinning technique (Bai et al., 2022) designed to reduce duplicated presence information within individual grid cells. This process retained all 23 occurrence localities as training data, with no more than one record falling in any single grid cell. By minimizing spatial autocorrelation and pseudoreplication in the model inputs in this manner, we obtained enhanced model calibration and more reliable predictions across the study region.

2.3.2. Multicollinearity analysis

Due to the potential interdependence among diverse factors, the incorporation of all environmental variables, geomorphic conditions, foraging conditions, and anthropogenic types in the model increases susceptibility to overfitting. To mitigate this concern, we performed correlation analysis for each environmental variables in ENMTools version 1.0.6 (Warren et al., 2021) elucidating the contribution rate of individual variables and retaining

solely those exhibiting more considerable contributions (Lu et al., 2020). The correlation analysis facilitate the identification of minor environmental variables generally exhibiting in between $|R| > 0.8-0.9$ leading to their exclusion (Bai et al., 2022; Lu et al., 2020).

2.3.3. Maxent Model and optimal configuration of variables

Maxent, an intricate machine learning methodology rooted in the principle of maximum entropy, is applied for the examination of species occurrence data in addition to environmental variables. The calibration phase of this framework holds paramount importance in guaranteeing the precise formulation of the model (Valavi et al., 2022). Its principal aim resides in determining the optimal parameter configuration for accurately encapsulating the targeted phenomenon through meticulous harmonization with the accessible dataset (Guga et al., 2021). The default predictions allow the Maxent model to be conservative; however, adjusting the model's parameters allows for the modification of Maxent's complexity, enhancing the precision of species distribution forecasts (Bai et al., 2022; Qiao et al., 2013; Smit et al., 2012). In this study, the Enmeval package in R was used to construct the Maxent model, which included a feature combination (FC) and a regularization multiplier (RM). The feature class comprised linear features (L), quadratic features (Q), product features (P), hinge features (H), and threshold features (T) (Bai et al., 2022; Valavi et al., 2023; Wan et al., 2020). Utilizing the six feature combinations provided by the Maxent model (L, H, LQ, LQH, LQHP, and LQHPT), a total of 30 combinations were generated. Furthermore, the study specified regularized multipliers ranging from 1 to 5, with an interval of 1 for each multiplier.

The Akaike information criterion corrected for small sample size (AICc) was used as an indicator of the RM and FC of the model (Carlson et al., 2017). The BNC occurrence records, and the above 10 environmental factors were imported into the Maxent model, and the other settings were as follows: RM and FC values under the optimal parameters were input, unity cross-validation was selected, and the jackknife method was chosen to test the importance of each environmental factor. The model prediction results were examined using the area under the receiver operating characteristic (ROC) curve (AUC) ranging from 0–1, and the closer the AUC is to 1, the greater the model prediction accuracy (Bai et al., 2022).

2.3.4. Model evaluation and habitat suitability classification

The AUC, commonly utilized in species distribution modelling, evaluates model performance in distinguishing between presence and absence sites. The NLR is computed by analysing the balance between "1 – specificity" (indicating the rate of falsely predicted absences or false positives) and "sensitivity" (representing the rate of accurately predicted presences or true positives, also termed "recall") across various thresholds used to categorize output probabilities into 0 and 1 (Valavi et al., 2022). The closer the value is to 1, the more suitable the species distribution. Species predictive distribution maps display species preferences for habitats as probabilities (0–1). Three criteria are often followed when choosing thresholds: objectivity, equivalence, and discriminative capacity (Liu et al., 2013). The choice of threshold value for categorizing SDM predictions as suitable versus unsuitable habitat is a key consideration.

Common approaches for threshold selection include minimizing omission errors (false negatives) or maximizing sensitivity/specificity to balance omission and commission errors (false positives) (W. Li & Guo, 2013). Researchers argue that the latter approach accounts for both error types better than the former approach (Zhang et al., 2018). Specifically, the "maximum training sensitivity plus specificity" (MTSS) threshold complies with the recommended principles of 1) maximizing predictive accuracy, 2) maintaining prediction objectivity, and 3) considering model complexity (Jiménez-Valverde & Lobo, 2007). By balancing sensitivity (true positive rate) and specificity (true negative rate), the MTSS threshold classifies habitats based on both omission and commission errors (Liu et al., 2013). Consequently, Zhang et al., (2018) applied four thresholds based on the MTSS value: unsuitable habitat was classified below the MTSS threshold; low suitability was classified between the MTSS and a value-balancing omission error; moderate suitability was classified between that and a threshold based on the projected habitat area; and high suitability was classified above the projected area threshold. In summary, balancing model sensitivity and specificity via the MTSS threshold, accounting for both omission and commission errors, enables objective classification of predicted habitat suitability (Liu et al., 2013; Zhang et al., 2018). In addition to utilizing AUC as a performance metric, we employed practical-based measures, notably TSS, to assess the efficacy of Maxent models in discerning between correct and erroneous predictions regarding species presence and absence (Allouche et al., 2006). Further elucidation on the application of TSS within the context of SDM can be found in a recent investigation conducted by Yoon & Lee, (2023), wherein TSS was employed to evaluate SDM models across various species using machine learning techniques.

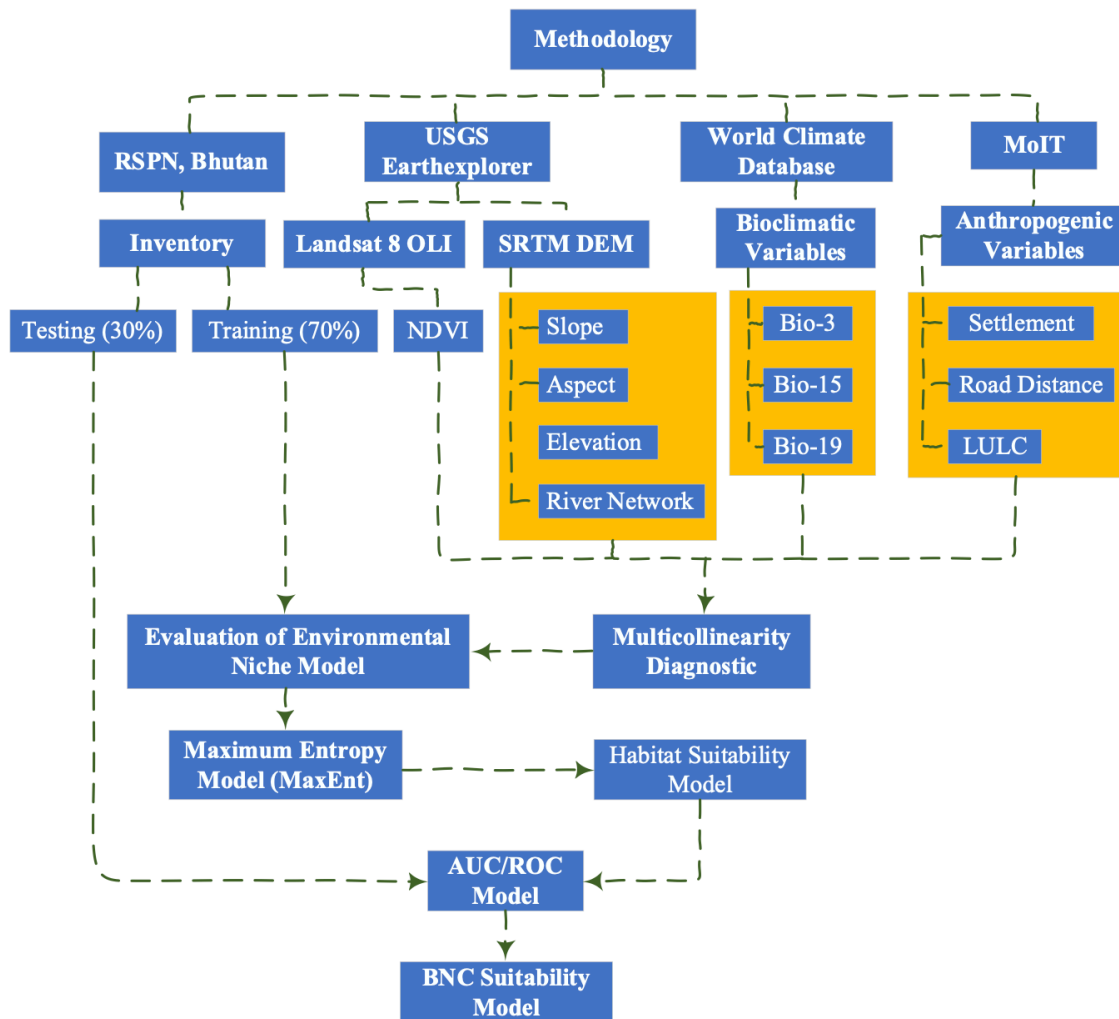


Figure 2. General flow chart of the Maxent model approach and methodology.

3. Results

3.1. Selection of bioclimatic and Environmental Variables

A Pearson correlation plot (r) was generated to visualize the relationships between bioclimatic variables and environmental factors, as demonstrated in Figure 3. Subsequently, environmental variables demonstrating $|r| < 0.8$ were selected for the evaluation of the ecological niche model via R software. To further refine the model, the jackknife method was applied to systematically eliminate environmental variables with a zero-contribution rate. Consequently, in the modelling process, three pivotal environmental factors (i.e., isothermally (Bio 3), precipitation seasonality (Bio15) and precipitation in the coldest quarter (Bio19)) were retained, encompassing specific geomorphic conditions, foraging conditions, and anthropogenic types.

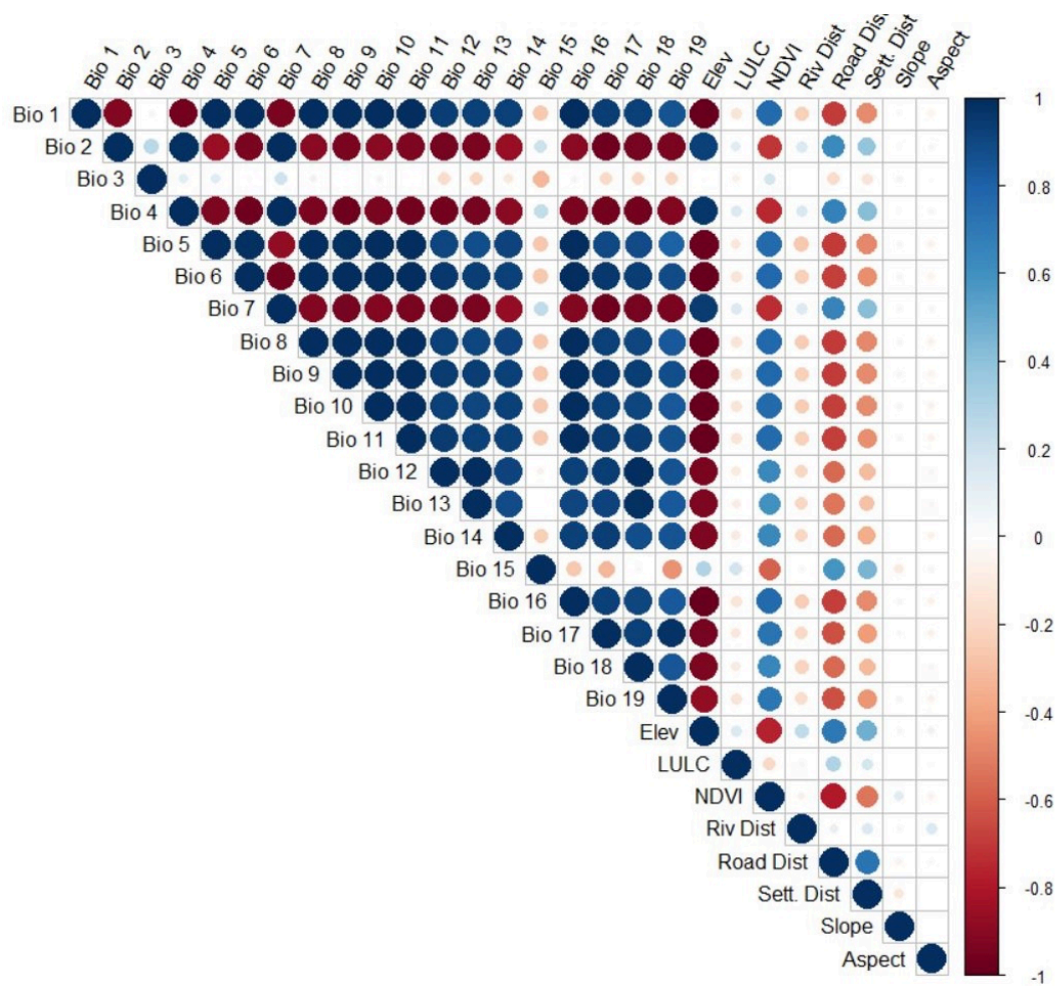


Figure 3. Correlation heatmap of the bioclimatic variables and environmental factors.

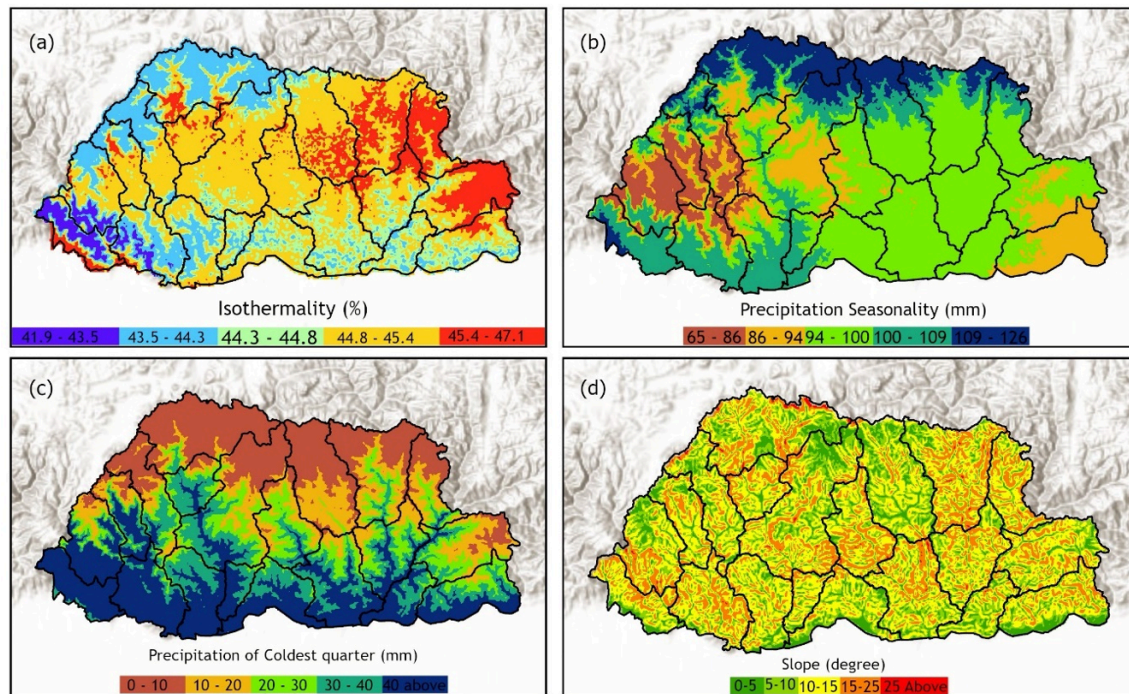


Figure 4 (a-d). Factor maps representing (a) isothermality (BIO-3), (b) precipitation seasonality (BIO-15), (c) precipitation in the coldest quarter (BIO-19), (e) slope, (d) distance from settlement, (f) road proximity, (g) river distance, (h) NDVI, (i) aspect and (j) landuse landcover.

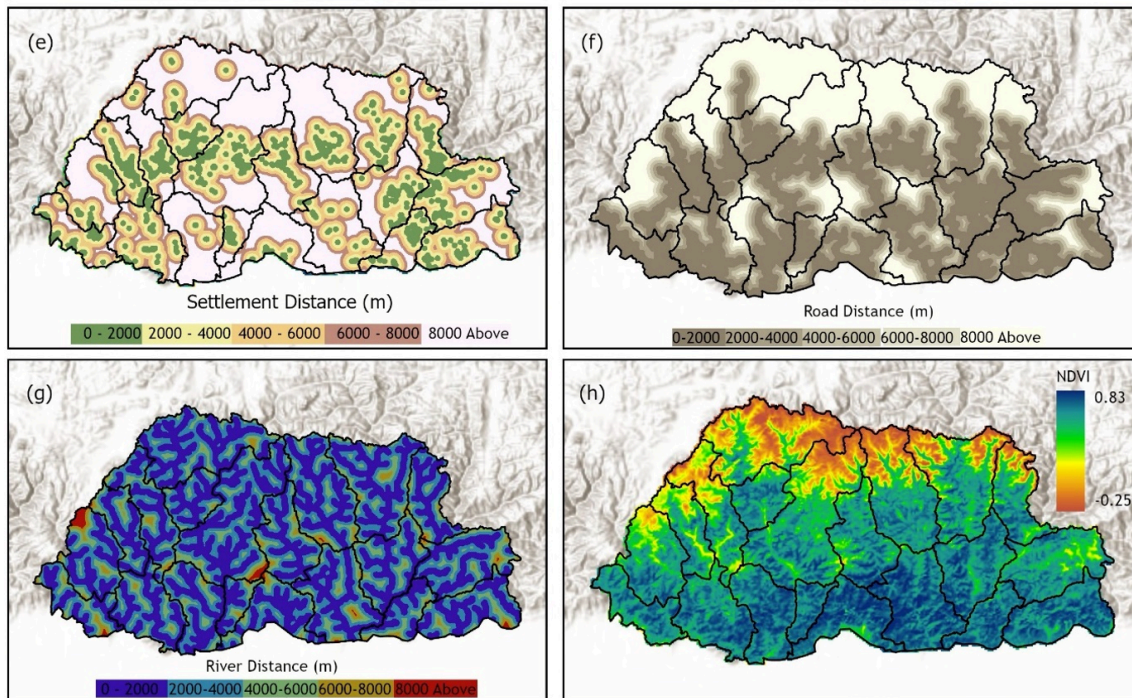


Figure 4 (e-h). Factor maps representing (a) isothermality (BIO-3), (b) precipitation seasonality (BIO-15), (c) precipitation in the coldest quarter (BIO-19), (e) slope, (d) distance from settlement, (f) road proximity, (g) river distance, (h) NDVI, (i) aspect and (j) landuse landcover.

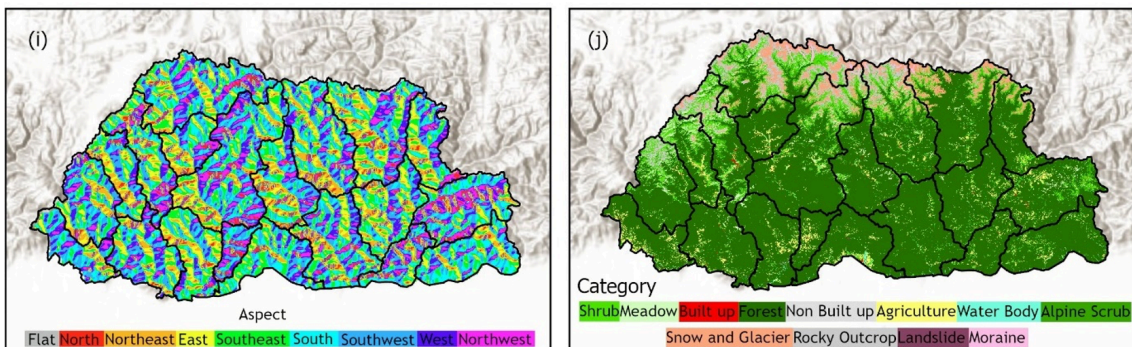


Figure 4 (i-j). Factor maps representing (a) isothermality (BIO-3), (b) precipitation seasonality (BIO-15), (c) precipitation in the coldest quarter (BIO-19), (e) slope, (d) distance from settlement, (f) road proximity, (g) river distance, (h) NDVI, (i) aspect and (j) landuse landcover.

3.2. Maxent Optimal Model and Accuracy Evaluation

Based on 23 occurrence records and 10 environmental factors, this study used the Enmeval package to allow Maxent to predict the potential distribution area of BNCs. The model with the lowest AICc value (i.e., $\Delta AICc = 0$) is considered

the best model out of the current suite of models (Muscarella et al., 2014). The Maxent algorithm uses default regularization settings to automatically fit appropriate complexities in species–environment relationships while avoiding overfitting. Specifically, model complexity is determined based on the number of presence locations during calibration, an approach for avoiding unnecessary parameters. However, customized tuning of key Maxent parameters can enhance model performance. Using the Enmeval R package, we conducted analyses to derive optimized feature class (FC) and regularization multiplier (RM) configurations for modelling BNC habitats. The top performing parameterizations, with FC set to "LQH" and RM equal to 3, produced a mean test AUC of 0.98 (Figure 5), indicating excellent ability to predict suitable versus unsuitable sites according to the evaluation data. In this manner, custom-set complexity avoided both underfitting and overfitting for an improved niche model. Furthermore, notwithstanding the scarcity of occurrence data, which typically yields high AUC values, the utilization of TSS emerges as a pivotal approach in SDM particularly for datasets with limited occurrences. TSS represents a pragmatic metric for evaluating model performance. Consequently, our study underscores the exceptional predictive capabilities of the model, as evidenced by an overall accuracy of 96%, sensitivity and specificity rates of 0.87 and 0.96, respectively, alongside a corresponding TSS value of 0.83.

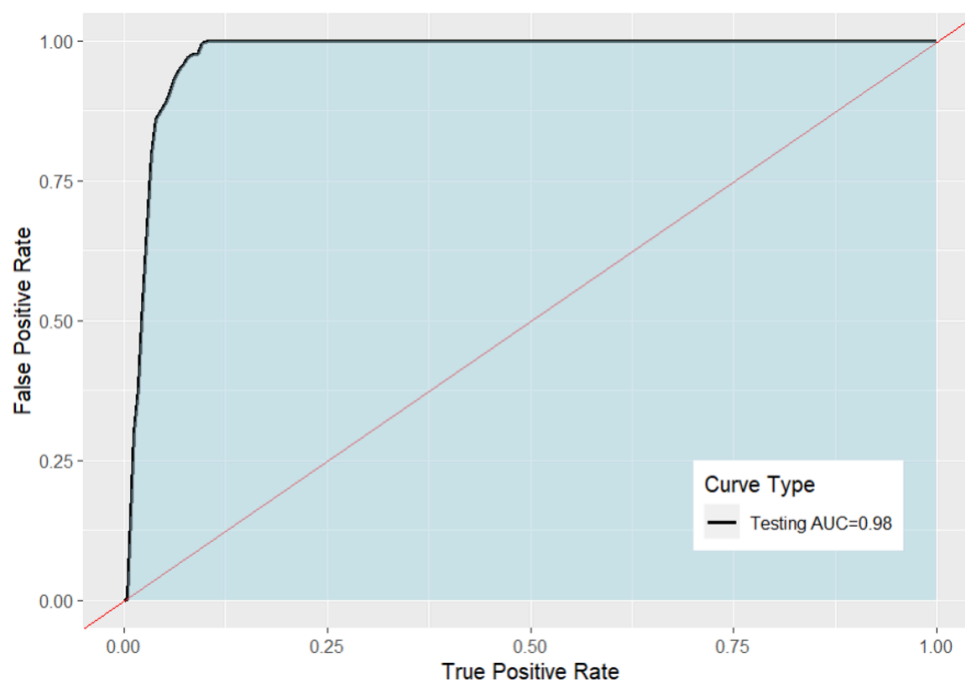


Figure 5. Performance evaluation (AUC) of the MaxENT-LQH-RM Model

3.3. Influence of Environmental Factors on the Distribution of BNC

To assess the significance of the bioclimatic variables and environmental factors influencing BNC habitat selection, jackknife analysis (Figure 6) was used to determine that certain environmental variables, as presented in Table 3, notably distance to settlement, NDVI, distance to road, and distance to river, may constitute the primary factors

affecting BNCs, with respective contribution rates of 31.7%, 20.5%, 20.2%, and 17.7%, collectively accounting for a cumulative contribution rate of 90.1%. Additionally, the secondary variables impacting the distribution of BNC included aspect, BIO-19, LULC, slope, BIO-15, and BIO-3, with contribution rates of 3.7%, 3.3%, 2%, 0.7%, 0.1%, and 0.1%, respectively, resulting in a cumulative contribution rate of 9.9%. This suggests that the influence on the suitability of BNCs is relatively minor. However, permutation importance, a measure that directly assesses variable importance through observing the effect on model accuracy when shuffling each predictor variable value generated by Maxent randomly, indicates that Bio15 holds zero importance in the habitat suitability of BNCs.

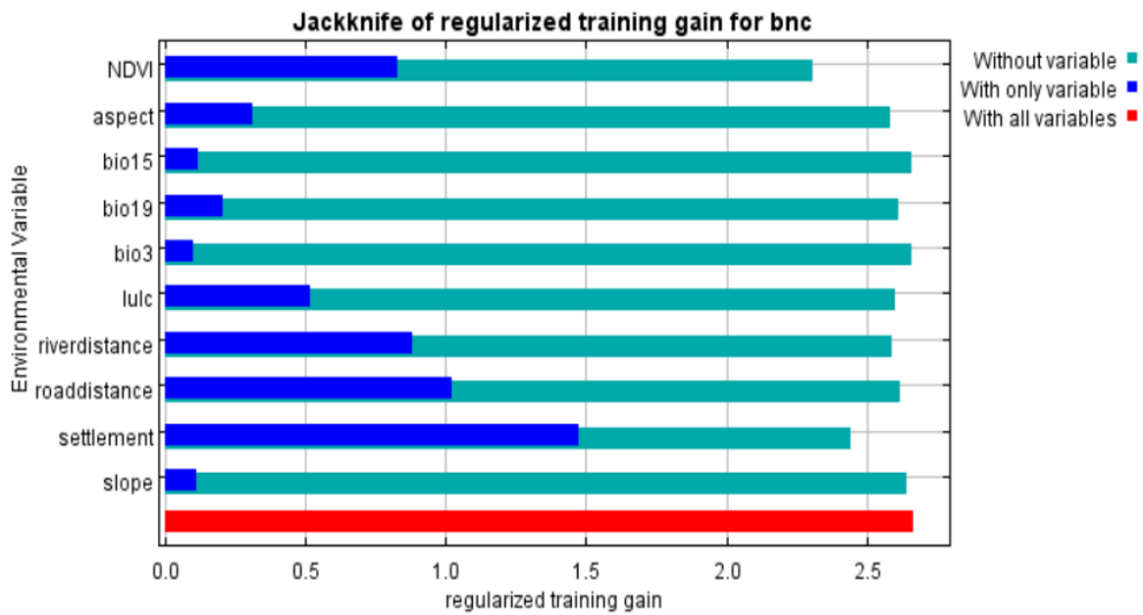


Figure 6. Importance of each variable evaluated using jackknife test.

Variable	Percent contribution	Permutation importance
Settlement	31.7	42.9
NDVI	20.5	41.9
Road distance	20.2	6.2
River distance	17.7	4.7
Aspect	3.7	1.2
LULC	2	0.7
Slope	0.7	0.9
Bio19	3.3	1.1
Bio15	0.1	0
Bio3	0.1	0.5

Table 3. Contribution of each of the variables in modelling

3.4. BNC Habitat Suitability Distribution

According to the Maxent model outcomes, the values for the MTSS and TPT were determined to be 0.175 and 0.357, respectively. Thus, delineating more suitable and less suitable habitats for BNCs was established at these thresholds: 0.175 and 0.357, respectively. To generate the habitat distribution map for the BNCs in Bhutan (see Figure 7), the model outputs were reclassified into four distinct habitat classes based on the specified thresholds, namely, highly suitable (1–0.5), moderately suitable (0.5–0.357), poorly suitable (0.357–0.175), and unsuitable (0.175–0). Subsequently, the area of each suitable distribution zone was computed individually. A statistical analysis revealed that out of the total area of 38,394 km², approximately 1.443% (equivalent to approximately 549 km²) constituted an extremely suitable habitat for BNCs. The moderate-suitable habitat encompasses approximately 660 km² or 1.735%, while the low-suitable habitat covers approximately 1102 km² or 2.897%. Additionally, areas deemed very low suitability accounted for 3358 km² or 7.887%, whereas unsuitable areas encompassed 32,725 km² or 86.037%.

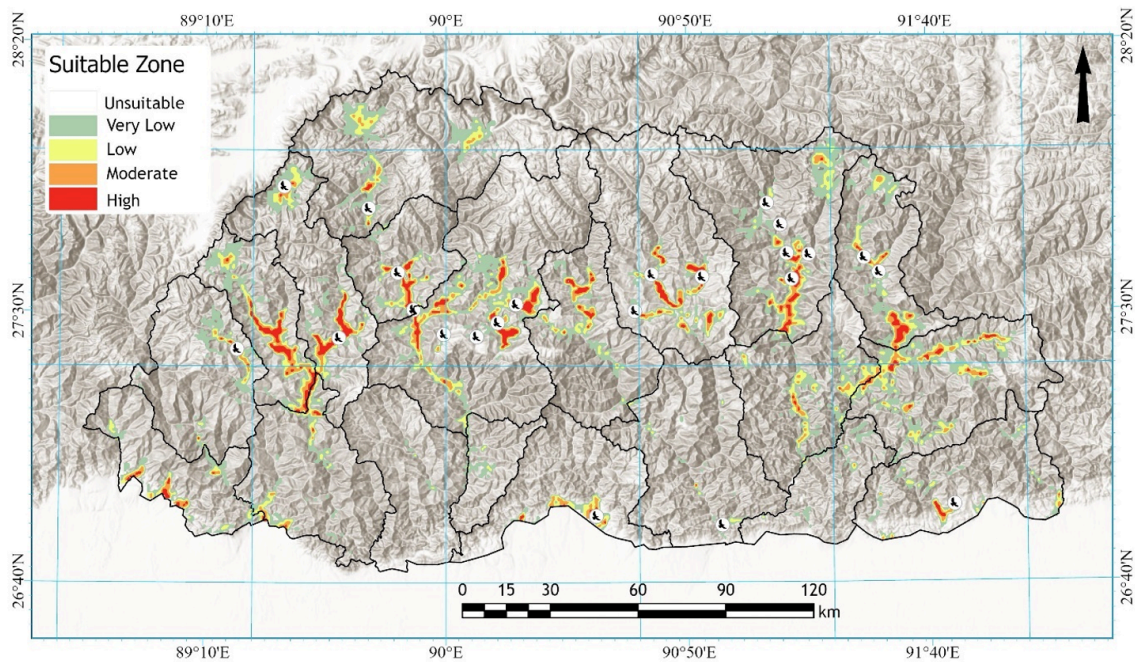


Figure 7. Habitat suitability map overlaid on the location of occurrences of BNCs across Bhutan.

3.5. Habitat suitability of BNCs within the PAN and BC

In Bhutan, there are 10 designated PANs alongside nine BCs, crucial regions necessitating preservation and safeguarding due to their role as habitats for numerous wildlife species. The combined expansion of these PANs amounted to 16,795.40 km², while the BCs encompassed an area of 2,659.52 km². Notably, as illustrated in Figure 8 and Table 4, the coverage of both PANs and BCs was relatively limited. Analysis of the findings revealed that merely 1.44% of Bhutan's total land area, equivalent to approximately 549 km², is deemed suitable habitat for BNCs. Further examination, incorporating the overlay of the PAN, revealed that approximately 0.74% of the land, translating to 51 km² of suitable habitat, lies within the confines of the PAN, while the rest of the area is outside the PAN and BC.

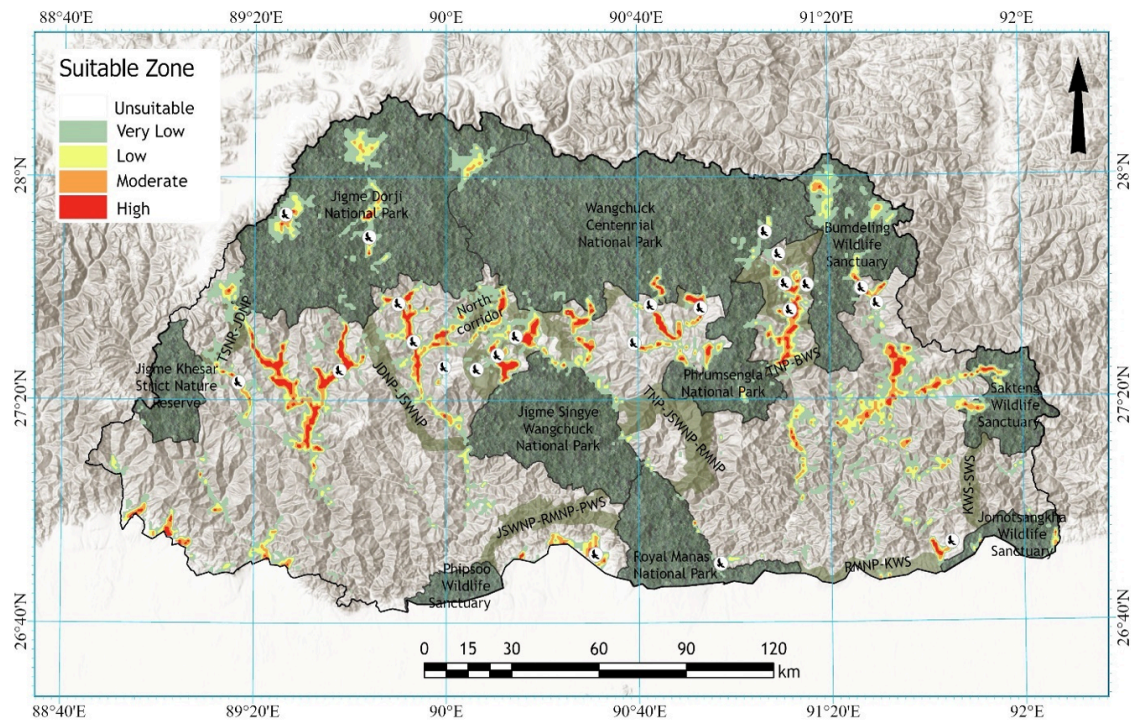


Figure 8. Habitat suitability map of BNCs constituting 10 PAN and 9 BCs across Bhutan. Light green represents the BC, and the darker green zone represents the PAN across Bhutan.

Suitability	Area (km ²)	% of Bhutan	Inside PAN (km ²)	Inside PAN (%)	Inside BC (km ²)	Inside BC (%)	Within PAN
Highly Suitable	549	1.443	34	0.24	17	0.5	51
Moderately Suitable	660	1.735	85	0.51	36	1.5	121
Low Suitable	1102	2.897	243	1.45	54	2	297
Very Low Suitable	3358	7.887	941	9.6	276	10	1217
Unsuitable Area	32725	86.037	14809	88.2	2306	86	17115

Table 4. Statistical summary of suitable and unsuitable habitats for BNCs in Bhutan within and outside the PAN and BC regions

3.6. Habitat Suitability of BNCs within Foraging Sites

The RSPN revealed that foraging sites of BNCs spread across the valleys of four districts: Wangduephodrang (Gangtey, Phobjikha, and Khotokha) in the western central region, Bumthang (Chumey, Chokhor, and Tang) in the central region, and Lhuentse (Dungkar) and Trashiyangtse (Bumdeling) in the eastern region. Of these four foraging sites, the valleys of Phobjikha in Wangduephodrang and Bumdeling in Trashiyangtse are the two major wintering habitats, of which Phobjikha hosts the largest population in the country. Figure 9 and Table 5 illustrate the spatial correlation between highly suitable sites, denoted by red-colored pixels, and foraging locations, as identified by the RSPN. Within these foraging areas, a cumulative area of 41.9 km² comprised highly suitable sites. Specifically, the Phobjikha, Gangtey, and Khotakha regions exhibited the most highly suitable sites, covering 29.84 km², followed by Chumey, Chokhor, and Tang, with 9.23 km²; Bumdeling in Tashi Yangtse, with 2.35 km²; and Dungkar in Lhuentse, with the smallest suitability area of 0.46 km².

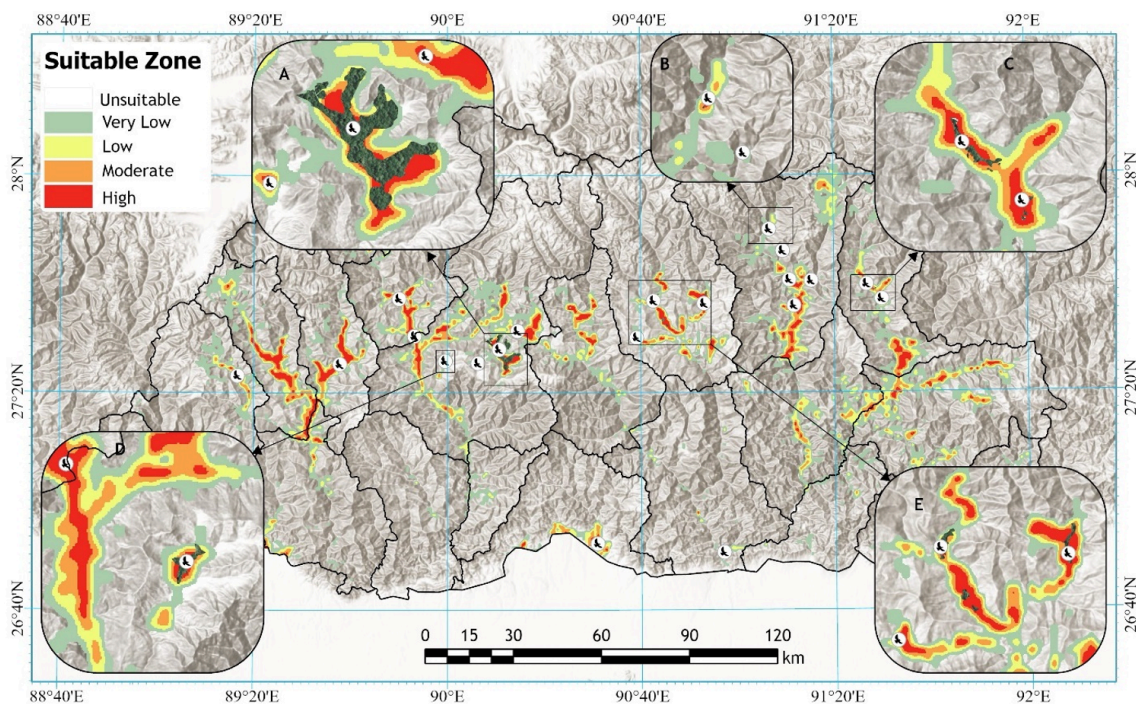


Figure 9. Habitat suitability map within foraging sites overlaid by the occurrence of BNCs. The foraging sites were maintained by the RSPN and RGoB across Bhutan overlaid on the suitability zone demarcated on each foraging roosting habitat.

Location	Dzongkhag	Foraging sites	Area of suitability (km ²)
A and D	Wangduephodrang	Gangtey, Phobjikha, and Khotokha	29.86
E	Bumthang	Chumey, Chokho and Tang	9.23
B	Lhuntse	Kurtoe (Dungkar)	0.46
C	Tashiyangtse	Bumdelling	2.35

Table 5. Areal statistics of highly suitable sites within foraging sites

3.7. Expansion and proposal for BNC conservative area across Bhutan

Upon examining the superimposition of the suitability zone with various factors influencing BNC habitat suitability, it becomes evident that the suitability zone closely corresponds with settlement distances within the 0-2000m buffered zone. This observation underscores the substantial impact of human anthropogenic activities on BNC habitat suitability.

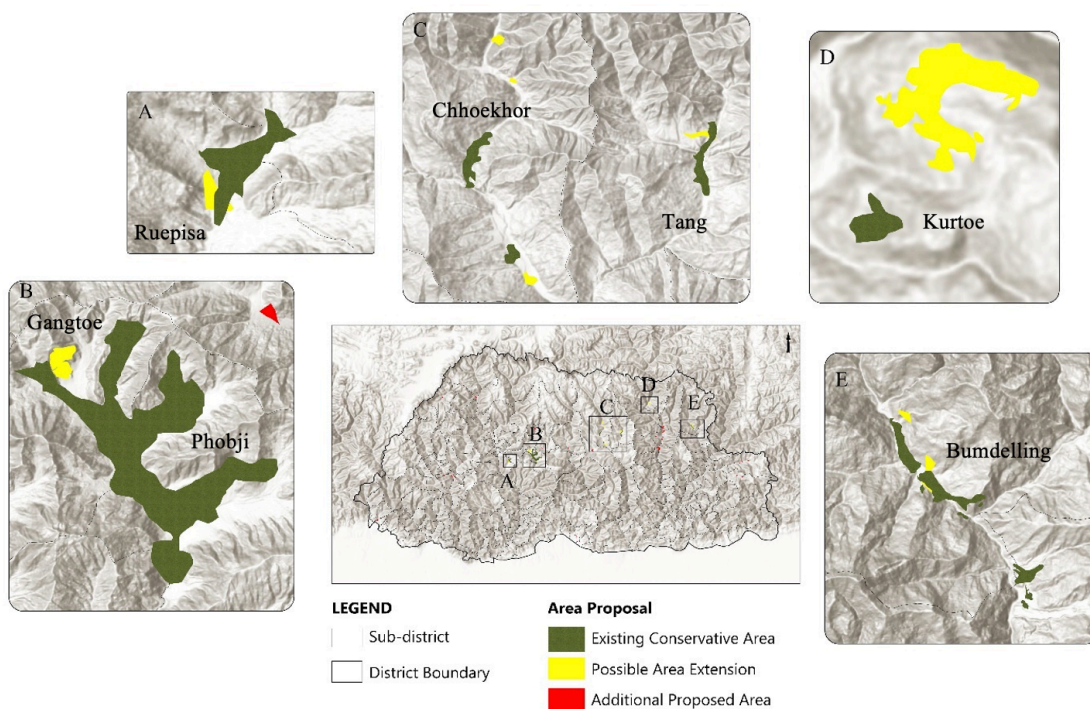


Figure 10. Illustration of existing foraging site and proposal for extension including newly proposed area for BNC habitat based on suitability zone.

To address the need for expanding conservation efforts, a comprehensive union analysis was conducted using the ArcGIS Pro platform. This analysis involved intersecting the existing conservation zone with the settlement buffered zone (0–2000m), followed by a further union with the high suitability zone. The results of this analysis shed light on the potential for expanding conservation areas. It was found that existing conservation areas at Phobji cannot be expanded due to overlapping with both the suitability zone and settlement areas (Figure 10B). However, opportunities for expansion exist for Gangtoe (Figure 10B), Ruepisa (Figure 10A), Chhoekhor and Tang (Figure 10C) conservation areas. Gangtoe conservation area could be extended by 1.15 km², from its current size of 2.88 km², Ruepisa's conservation area by approximately 0.32 km² from its current size of 2.68 km², while Tang's conservation area could be expanded by 0.37 km² from its existing 3.33 km². Additionally, the Kurtoe and Bumdelling conservation areas totaling 0.08 km² and 2.89 km² could be extended by an additional 0.43 km² and 0.36 km², respectively (Figure 10D and E).

Despite the challenges posed by the absence of roosting sites in certain areas such as Sephu in Wangduephodrang, Chuzagang and Umling in Sarpang, Doga in Paro, Chargharay in Samtse, Merak and Sakteng in Trashigang, and Tshenkhar, Menbi, Minjay, and Khoma in Lhuntse districts, conservation efforts can still be pursued. These efforts aim to preserve and protect the habitats of the BNC species. Detailed information regarding the conservation potential of these areas is provided in Table 6 below.

District	Gewog	Area (km ²)	Remarks
Sarpang	Chuzagang	0.64	
	Umling	0.53	
Paro	Doga and Benye	1.85	
Samtse	Chargharay	1.13	
Trashigang	Merak	1.12	Portion of it fall under PAN
	Sakteng	1.53	PAN
Lhuntse	Minjay	1.84	
	Menbi	0.43	
		Tsenkhar	2.51
		Khoma	1.49
Bumthang	Chhoeckhor	0.47	PAN
Wangduephodrang	Dangchu	1.04	
Thimphu	Lingzhi	0.50	PAN
Laya	Goenkhatoe	0.87	PAN

Table 6. Possible Conservative area for BNC

4. Discussion

Achieving an optimal balance of model complexity is crucial for enhancing interpretability, with adjustments made using feature combinations (FCs) and regularization multipliers (RMs). In this study, FC = LQH and RM = 3 were the best fits for mapping BNC habitat suitability in Bhutan. The optimal combination of LQH–RM to Maxent model provide high accuracy in term of AUC and TSS with 0.98 and 0.83 respectively. The suitability mapping revealed that only a small fraction of Bhutan's land area is highly suitable for BNC, with the majority being unsuitable. Subsequent analysis within the PAN indicated varying levels of suitability across different regions, with Wangduephodrang identified as a significant habitat hotspot. Utilizing foraging site data provided further insights, confirming that Wangduephodrang is a key area for BNC sightings.

The spatial distribution of BNC habitat prominently indicates high suitability in the vicinity of the Paro district, as evidenced by the Maxent modelling approach, which may be limited in the data repository of the RSPN. However,

according to the information provided by the RSPN (<https://www.rspnbhutan.org/black-necked-crane-sighting-at-khamdra-paro/>), the observed visit time for BNCs occurred in March 2021, a fact subsequently corroborated by forestry personnel. As articulated by Namgay & Wangchuk, (2016), conservation threats to BNCs primarily stem from biological factors, including habitat loss, disturbance, competition, and insufficient scientific inquiry. Furthermore, agricultural practices, particularly the use of chemical agents and alterations in cultivation methods not favoured by BNCs, pose additional challenges. A comparable scenario was evident in the Kangpara under Trashigang district, as documented on the RSPN website (<https://www.rspnbhutan.org/black-necked-crane-in-kangpara-trashigang/>) in 2011; however, our model suggested that this habitat was highly suitable for BNC foraging and roosting. The apparent absence of BNCs subsequent to their initial appearance may be attributed to factors outlined by Namgay & Wangchuk, (2016).

One major determinant of BNC habitat suitability in Bhutan may be the availability of diverse food sources. As indicated in Figure 10, the majority (60%) of the observed BNC roosting locations were in agricultural fields, followed by meadows. Only a small fraction of sightings occurred in shrublands or around waterbodies. These results align with previous findings by Namgay & Wangchuk (2016), who highlighted the importance of crop and grassland habitats for the species. The predominance of agricultural areas, which provide abundant waste grain and associated vegetation, suggests that food availability strongly influences the regional distribution patterns of BNCs in Bhutan. Nonetheless, in addition to water and food availability, reflected variables such as settlement distance, river distance and precipitation metrics were also found to significantly impact crane habitat suitability, aligning with prior research findings (Yan et al., 2018).

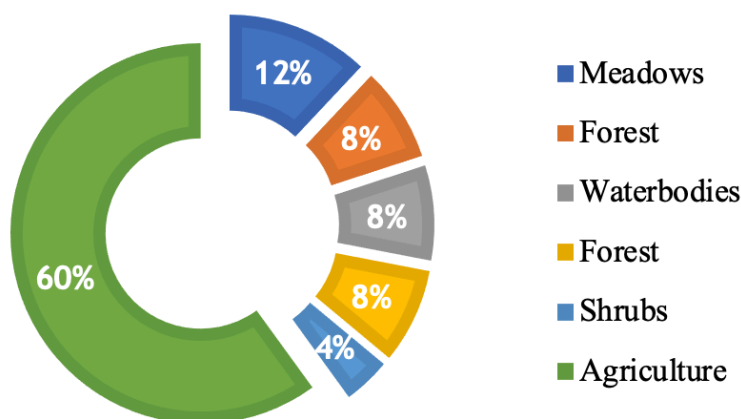


Figure 11. Roosting sites of BNCs overlaid on a land use map depicting the location of BNCs in the land use category.

Additionally, the NDVI and maximum temperature emerged as crucial determinants, highlighting the importance of vegetation cover and climatic conditions. The favorable landscape and climatic conditions of Bhutan, particularly in

regions such as Phobjikha, Bumdeling, and Bumthang, were found to be highly conducive to black-necked crane wintering, reflecting the species's preference for Himalayan habitats (RSPN, 2021).

In an endeavor to rehabilitate essential habitat for BNC in Bumdeling, the RSPN collaborated with local farmers, the International Crane Foundation, and the Bhutan Wildlife Service to implement a habitat restoration initiative (DoFPS, 2021). This collaborative effort entails the restoration of flood-damaged paddy fields by clearing flood debris and implementing proper terracing techniques. As a result of this pilot program, 10 acres of habitat were successfully restored, with the intention to extend these endeavors more broadly contingent upon the program's continued success in improving crane habitat, as reported by RSPN, (2021). This collaborative approach harnesses community involvement to effectuate on-the-ground alterations beneficial to both agriculturalists and wildlife.

Furthermore, by focusing on habitat suitability through scientifically informed initiatives, such as those demonstrated in Bumdeling, the rehabilitation of BNC habitat sites could be further enhanced. Thus, the current suitability zones serve as valuable reference data for enhancing the habitat of BNCs within Bhutan. These zones provide crucial insights into the areas where BNCs are likely to thrive, offering a foundation upon which conservation efforts can be built. By utilizing the Maxent model outputs, conservationists and policymakers can identify priority areas for habitat restoration and protection measures, ensuring that the resources are directed toward areas with the highest potential for supporting BNC populations, ultimately contributing to the long-term conservation and sustainability of this species within Bhutan. This emphasis on suitability ensures the maintenance of suitable breeding and wintering grounds, thereby ensuring the continued presence of this vulnerable species within Bhutan.

5. Conclusion

Utilizing the Maxent model, black-necked crane occurrence points were collected, processed, and incorporated with pertinent environmental predictor layers to delineate habitat suitability across the study region. The optimized Maxent model, tuned via sample size-adjusted feature classes and regularization parameters, exhibited strong predictive ability, as quantified by the AUC test and TSS evaluation metrics. Among the most influential variables for predicting suitability were distance to settlement, NDVI, distance to road, and distance to river, which collectively accounted for more than 90% of the model explanatory capacity.

The modelling identified additional highly suitable areas, such as the Paro district. However, recent observational data from the RSPN recorded BNC sightings in Paro only as transient visitors in March 2021, suggesting that suitability alone does not ensure habitat usage. As noted by other researchers, threats such as habitat loss and agricultural intensification may preclude cranes from occupying otherwise suitable sites. Similar factors may explain why locations such as Kangpara under Trashigang have not shown sustained BNC presence despite appearing climatically and topographically appropriate.

Analyses of roosting locations further demonstrated that food availability is a major driver of habitat selection, with the majority of BNCs roosting in agricultural areas and meadows where waste grain is abundant. While vegetation

and climate variables such as precipitation also contribute, the provision of foraging resources seems to play a key role. Ongoing habitat restoration initiatives in the Bumdeling region exemplify cooperative efforts to improve habitat quality through actions such as flood debris clearance and terracing in paddy fields.

Overall, these environmental niche suitability maps provide valuable guidance on the current and potential BNC ranges in Bhutan. Conservation efforts can utilize this information to direct management resources toward the highest priority zones for protecting and rehabilitating environments to sustain vulnerable crane populations. Maintaining suitable breeding and wintering grounds will be key to ensuring the continued presence of this species. To ensure the effective long-term protection of BNC populations, the expansion of protected areas and habitat monitoring systems should constitute top priorities. Additionally, sustained ecological research on how environmental modifications influence cranes can inform adaptive management approaches. As conditions shift, updated scientific knowledge regarding climate change impacts, land use patterns, and other processes will prove vital for modifying conservation actions accordingly. Ultimately, multistakeholder efforts emphasizing proactive habitat conservation, from designating crucial sites such as breeding grounds to enacting policy safeguards, offer the best avenue for preserving Bhutan's vulnerable BNCs. By taking such coordinated measures today, the likelihood of sustaining healthy crane numbers across their current and potential future range can be maximized.

The limitations of our work are primarily rooted in the complexities of land use status in proposed areas for expansion of the existing conservation areas for the BNC. This raises concerns about the potential for legal disputes over land ownership and usage rights. Furthermore, the scarcity of existing foraging and roosting sites for the BNC poses challenges in providing sufficient data for training machine learning models, thereby hindering efforts to fine-tune and enhance the robustness of these models.

Addressing these limitations requires careful consideration of legal frameworks governing land use and ownership rights, as well as efforts to identify and establish additional foraging and roosting sites for the BNC. This may involve collaborations with local communities, government agencies, and conservation organizations to navigate legal complexities and ensure sustainable conservation practices.

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